Nutritional Ecology of the Formosan Subterranean Termite (Isoptera: Rhinotermitidae): Feeding Response to Commercial Wood Species

JUAN A. MORALES-RAMOS AND M. GUADALUPE ROJAS

Formosan Subterranean Termite Research Unit, USDA–ARS, Southern Regional Research Center, New Orleans, LA 70124

J. Econ. Entomol. 94(2): 516–523 (2001)

ABSTRACT The feeding preferences of the Formosan subterranean termite, *Coptotermes formosanus* Shiraki, were tested in three separate experiments on 28 different wood species. Experiment 1 was a multiple-choice test designed to test relative preferences among 24 wood species commercially available in New Orleans, LA. Experiment 2 was a similar study designed to test relative preferences among 21 wood species shown or reported to be unpalatable to the Formosan subterranean termite. Experiment 3 was a no-choice test to examine the feeding deterrence of the 10 least preferred wood species. Preference was determined by consumption rates. Birch (*Betula alleghaniensis* Britton), red gum (*Liquidambar styraciflua* L.), Parana pine [*Araucaria angustifolia* (Bert.)], sugar maple (*Acer saccharum* Marsh.), pecan (*Carya illinoensis* Wangenh.), and northern red oak (*Quercus rubra* L.) were the most preferred species by *C. formosanus* in order of consumption rate. All of these species were significantly more preferred than southern yellow pine (*Pinus taeda* L.), widely used for monitoring. Sinker cypress [= old growth bald cypress, *Taxodium distichum* (L.)], western red cedar (*Thuja plicata* Donn), Alaskan yellow cedar (*Chamaecyparis nootkatensis* D. Don), eastern red cedar (*Juniperus virginiana* L.), sassafras [*Sassafras albidum* (Nutt.)], Spanish cedar (*Cedrella odorata* L.), Honduras mahogany (*Swietenia macrophyla* King), Indian rosewood (*Dalbergia latifolia* Roxb.), Honduras rosewood (*D. stevensonii* Standl.), and morado (*Machaerium* sp.) induced significant feeding deterrence and mortality to *C. formosanus.* The last eight species produced 100% mortality after 3 mo.

KEY WORDS *Coptotermes formosanus,* subterranean termite, feeding-preference, deterrence, wood

SINCE ITS INTRODUCTION into the United States during the 1960s, the Formosan subterranean termite, *Coptotermes formosanus* Shiraki, has been one of the most destructive termites in the continental United States (Beal 1987). It is estimated that *C. formosanus* cause damage of several millions of dollars annually (Su and Tamashiro 1987, Su and Scheffrahn 1990) to houses, other buildings, utility poles, railway sleepers, boats and ships, paper, and living trees (Edwards and Mill 1986). This species is more destructive than native subterranean termites (*Reticulitermes* spp.) because of the larger colonies and foraging territories (Su and Tamashiro 1987, Su and Scheffrahn 1988). One of the characteristics of *C. formosanus* is its ability to attack several species of living trees (La Fage 1987, McMichael 1998), which makes it particularly destructive in large cities such as New Orleans, LA. High winds produced by storms can induce the fall of trees structurally weakened by the termites, producing indirect damage to property and injury to people.

Many studies have reported differences in feeding rates and survival of subterranean termite workers in no-choice (force) feeding tests with different species of wood (Smythe and Carter 1969, 1970a; Mannesmann 1973; Su and Tamashiro 1986; Waller et al. 1990; Grace and Yamamoto 1994). Smythe and Carter (1969) reported that *Reticulitermes flavipes* (Kollar) consumed significantly lower quantities of redwood [*Sequoia sempervirens* (Mierb.) Endl.], and bald cypress [*Taxodium distichum* (L.) Rich.] than nine other wood species in a choice test. However, when reared on sawdust the differences in wood consumption were not statistically significant (Smythe and Carter 1969). The preference for some wood species such as redwood, black cherry (*Prunus serotina* Ehrh.), and black walnut (*Juglans nigra* L.) changed when termites were presented with choices (Smythe and Carter 1970a). *C. formosanus* consumed comparatively more redwood in force-feeding tests than in a multiple-choice test (Smythe and Carter 1970a). Black cherry was eaten comparatively more heavily by *C. formosanus, R. flavipes,* and *R. virginicus* (Banks) when presented alone than when choices were available (Smythe and Carter 1970a).

The presence of allelochemicals in wood such as terpenoids, quinones, phenolics, and flavonoids has been associated with termite repellence and toxicity (Scheffrahn 1991). Loblolly pine wood was less repellent and toxic to *C. formosanus, R. flavipes,* and *R. virginicus* after being oven-dried at 105°C for 24 h.

These differences are explained by the loss of volatile compounds that tend to be either toxic or repellent to subterranean termites (Smythe and Carter 1970a, 1970b).

In a multiple choice test with 21 wood species, Mannesmann (1973) found that *C. formosanus* preferred western red cedar (*Thuja plicata* Don) and southern yellow pine (*Pinus* sp.) over the rest of the wood species. Because all of the woods tested were dried at 105°C for 20 h before exposure, preference of *C. formosanus* to the 21 species tested may have been altered due to the loss of volatile chemicals (Smythe and Carter 1970a). In no-choice tests with six wood species, Su and Tamashiro (1986) found that western red cedar and redwood were the most resistant, inducing the highest mortality and showing the lowest consumption (Su and Tamashiro 1986).

The objectives of this study were to design a multiple-choice test to study the preferences of *C. formosanus* with minimum changes in chemical characteristics of the wood, to determine the commercial wood species that are the most preferred by *C. formosanus* to recommend their use for monitoring termite activity, to identify wood species with higher relative resistance than southern yellow pine (*Pinus taeda* L., *P. echinata* Miller, and *P. palustris* Miller) suitable for use in construction, and to determine whether one or more commercial wood species poses true resistance to *C. formosanus* damage.

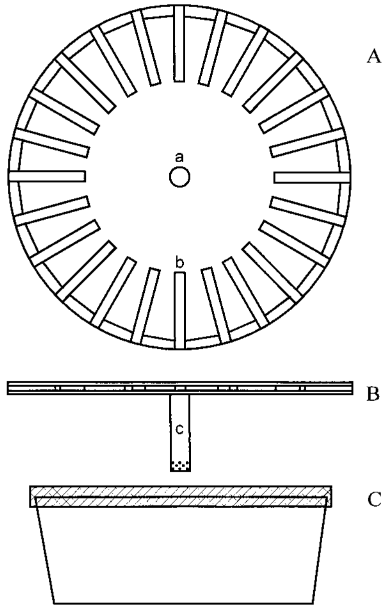

Fig. 1. Design of the multiple-choice test device. (A) Multiple-choice arena (45. 7 cm in diameter) with central access opening (a) (2. 5 cm in diameter) and 24 divisors (b) (10 by 1. 3 cm) creating 24 chambers. (B) Lateral view of the arena showing a 10-cm connecting PVC pipe (c), which allowed the termites access to the arena. (C) Plastic box containing a termite nest. Connecting pipe is introduced into the plastic box contacting the soil inside.

Materials and Methods

Experimental Design. A multiple-choice test was designed to compare *C. formosanus* feeding preferences of commercial wood species. A multiple-choice arena was designed for this purpose. The arena consisted of a circular base (45.7 cm in diameter) of Lexan with a central access hole (2.5 cm in diameter) and 24 dividers (10 by 1.3 cm) uniformly distributed around the base (Fig. 1A). The access hole was connected vertically to a plastic Rubbermaid box (40 by 27.5 by 14 cm, Wooster, OH) containing an active termite group (described below) by a 10 cm PVC pipe (3.5 cm o.d.) (Fig. 1 A and B). The 12 chambers created by the dividers were sealed to the exterior with pieces of Lexan (4.5 by 1.3 cm, GE Structured Products, One Plastics Avenue, Pittsfield, MA) and connected to the central access hole by 10 cm long pieces of flexible PVC tube (1 cm O.D.). The arena was covered by a second circular piece of Lexan, which was kept in place by eight medium-sized paper clamps.

Termite holding containers were constructed by adding 5 liters of a mix of topsoil (Hyponex, Marysville, OH) and sand (1:1) to the plastic boxes. One liter of deionized water and 5 g of polyacrilamide (T-400, Terawet, San Diego, CA) were added to each box to maintain humidity. A piece of corrugated cardboard (10 by 5 cm) was added to provide food to the termites during the adaptation process. A total of 2,200 workers and 440 soldiers of *C. formosanus* was added to each holding container. These numbers were selected to replicate a ratio of 1:5 soldiers:workers (16.6% soldiers) as observed in the colonies collected from the field. Termites were collected from the laboratory colonies by exposing soaked pieces of corrugated cardboard to the termites for 6–24 h. The pieces of cardboard were taken to the laboratory where termites were extracted and counted using an aspirator connected to a vacuum source. This method favors the collection of foraging workers over tending workers, which remain inside the nest. Workers and soldiers collected by this method varied in size and age, but this variation was not measured.

Biological Material. Large sections of Formosan subterranean termite nests were collected from three different locations within the New Orleans metropolitan area. Three different nests were collected from City Park in June 1998, one from a house in Algiers in August, and one from a house in Gretna in October. Each nest collected was assumed to belong to different termite colonies because the collection sites were separated by at least 2 km. The nests were kept in polyethylene trash cans in a room held at 25–30°C and 50–80% RH. Termites were collected from these nests by placing pieces of soaked cardboard inside the trash cans as described above. Termites also were collected from a colony located within the research station (Southern Regional Research Center) by using the same method inside a buried bucket next to an infested oak tree. Termites were added to the termite holding containers as described above and kept in

Table 1. Wood species tested for preference by *C. formosanus*

Common name	Scientific name	Key	Experiment
Southern yellow pine[a]	*Pinus taeda* L.	SYP	1, 3
Ponderosa pine[a]	*Pinus ponderosa* Laws.	PoP	1, 2
Douglas fir[a]	*Pseudotsuga menziesii* (Mirb.)	DoF	1
Bald cypress[a]	*Taxodium distichum* (L.)	BaC	1, 2
Sinker cypress[b]	*Taxodium distichum* (L.)	SiC	1, 2, 3
Redwood[b]	*Sequoia sempervirens* (D. Don)	ReW	1, 2
Western red cedar	*Thuja plicata* Donn		
From Western United States[a]		WRC	1, 2, 3
From Canada's West coast[c]			
Heartwood		WRh	2
Sapwood		WRs	2
Alaskan yellow cedar	*Chamaecyparis nootkatensis* (D. Don)		
Commercial wood from Western Canada[b]		AYC	2, 3
Wood stored for 6 yr[b]		AY6	2
Wood stored for 8 yr[b]		AY8	2
Wood exposed to the environment for 9 yr[b,d]		AY9	2
Eastern red cedar[e]	*Juniperus virginiana* L.	ERC	2, 3
Parana pine[e]	*Araucaria angustifolia* (Bert.)	PaP	1
Sugar maple[e]	*Acer saccharum* Marsh.	Map	1
American ash[e]	*Frexinus americana* L.	Ash	1
Black walnut[e]	*Juglans nigra* L.	Wal	1
Pecan[e]	*Carya illinoensis* (Wangenh.)	Pec	1
Yellow poplar[a]	*Liriodendron tulipifera* L.	YeP	1
Sassafras[e]	*Sassafras albidum* (Nutt.)	Sas	1, 2, 3
Red gum, sweetgum[e]	*Liquidambar styraciflua* L.	ReG	1
Basswood[e]	*Tilia americana* L.	Bas	1, 2
White oak[e]	*Quercus alba* L.	WhO	1
Northern red oak[e]	*Quercus rubra* L.	ReO	1
Yellow birch[e]	*Betula alleghaniensis* Britton	Bir	1, 3
Black cherry[e]	*Prunus serotina* Ehrh.	Che	1, 2
Osage orange[e]	*Maclura pomifera* (Raf)	OsO	2
Honey locust[e]	*Gleditsia triacanthos* L.	HoL	2
Indian rosewood[b]	*Dalbergia latifolia* Roxb.	InR	1, 2, 3
Honduras rosewood[e]	*Dalbergia stevensonii* Standl.	HoR	2, 3
Morado[e]	*Machaerium* sp.	Mor	2, 3
Spanish cedar[b]	*Cedrela odorata* L.	SpC	1, 2, 3
Honduras mahogany[b]	*Swietenia macrophylla* King	Mah	1, 2, 3
Balsa[e]	*Ochroma lagopus* (Cav.)	Bal	1

Blocks cut from all wood species originated from 2 separate wood boards (per species) purchased with at least 2 mo of difference, except for osage orange and honey locust which originated from a single board. Sinker cypress is the same species as the bald cypress but this commercial name refers to wood from old trees (500 yr or older) and mostly heartwood.

[a] Mostly sapwood.
[b] Mostly heartwood.
[c] Western red cedar from Canada was subdivided in sapwood and heartwood.
[d] Vancouver, British Columbia, Canada.
[e] Both sapwood and heartwood.

environmental chambers at 27°C, 98% RH, and constant darkness.

Feeding Preferences of Selected Commercial Wood Species (Experiment 1). The first experiment was a preference test of commercial wood species available in the New Orleans area. The wood species included in this experiment are listed in Table 1. All of the wood species used in experiment 1 were obtained locally.

Wood blocks (75 by 20 by 5 mm) were cut from each of the 24 wood species. The blocks were dried at 58°C in a vacuum oven at 50.84 cm of mercury for 24 h to minimize chemical degradation. The dry blocks were placed in an environmental chamber at 27°C and 98% RH for 30 min to stabilize their weight and weighed in a precision balance (Mettler Toledo AB204, Greifensee, Switzerland). A weighed block of each wood species was placed randomly in each of the 24 compartments of 20 multiple-choice arenas. The randomization was done by using the random number generator of MS Excel software (MicroSoft, Redmond, WA).

A total of 20 termite groups collected from six different colonies of *C. formosanus* was used in this experiment. This experiment was replicated four times, randomizing the distribution of the wood species in each repetition. However, placement of wood species from one repetition to the next was not completely random because a wood species was not placed in the same compartment from one replication to the next. This was necessary to avoid bias resulting from learning by the termite workers because colonies were not changed between repetitions.

The wood blocks were exposed to the artificial termite nests at 27°C, 98% RH, and total darkness. After a period of exposure of 40 d the multiple-choice arenas were opened to extract the wood blocks. The blocks were cleaned, dried, stabilized, and weighed using the method described above. The amount of wood consumed was determined by the difference in weight observed in the blocks before and after exposure to the Formosan termites. Consumption rate in milligrams per day was calculated by dividing the consumed weight by the days of exposure.

The mean consumption rate was compared between treatments by using the contrast option of the GLM procedure of JMP software (SAS Institute 1995). Deviations from normality arising from the large number of zero values were corrected by averaging the means of consumption rates among the four repetitions. This produced a total of 20 means per treatment. The GLM contrast option was used to compare means, which calculates Student *T* values of paired means.

Response to Less Preferred Wood Species (Experiment 2). A different set of wood choices was used in this multiple-choice experiment. The purpose of this experiment was to test preferences by Formosan termites among wood species that have been shown to be relatively less preferred. The 11 least preferred wood species from experiment 1 were incorporated in experiment 2 plus an additional 10 choices reported or presumed to possess relative resistance to termite damage. Resulting in a total of 21 choices (Table 1). Most of these wood species were obtained locally except for the Alaskan yellow cedar, *Chamaecyparis nootkatensis* (D. Don) (AYC, AY6, AY8, and AY9) and western red cedar 2, *Thuja plicata* Donn (WR2), which were obtained from British Columbia (Island Imports, Duncan, British Columbia, Canada), and honey locust, *Gleditsia triacanthos* L. (HoL) and osage orange, *Maclura pomifera* (Raf) (OsO), which were obtained from Illinois. The multiple-choice design, the method for measuring wood consumption, and the statistical analysis were as described in experiment 1.

Natural Resistance of Least Preferred Wood Species (Experiment 3). This experiment was a no-choice study to test the natural resistance of the least preferred wood species. Ten wood species that showed the lowest consumption in experiment 2 were selected for this study. The wood species selected included Alaskan yellow cedar; Honduras rosewood, *Dalbergia stevensonii* Standl.; Indian rosewood, *Dalbergia latifolia* Roxb.; morado, *Machaerium* sp.; Spanish cedar, *Cedrela odorata* L.; Honduras mahogany, *Swietenia macrophylla* King; eastern red cedar, *Juniperus virginiana* L.; western red cedar; sassafras, *Sassafras albidum* (Nutt.); and sinker cypress, *Taxodium distichum* (L.). Southern yellow pine (*Pinus taeda* L.) and yellow birch (*Betula alleghaniensis* Britton) were included in this experiment as controls (no resistant), totaling 12 species (Table 1).

The experimental design consisted of groups of 250 *C. formosanus* maintained in two stacked petri dishes connected by a central hole. The lower dish (150 by 25 mm) was filled with 200 ml of sand and top soil mix (1:1) (passed trough a no. 16 sieve), 100 ml of water, and 1 g of polyacrilamide. The bottom of the top dish (150 by 15 mm) was glued using all purpose hot-glue (Product No. BAP5–4, Arrow Fastener, Saddle Brook, NJ) to the cover of the lower dish and then connected vertically by melting through a 10-mm hole with a soldering iron. The lower dish functioned as a nesting site and the top dish as a foraging arena. Termites were collected from six different colonies as described above.

A block measuring 10 by 15 by 30 mm of one of the 12 wood species was placed on the top dish of each experimental unit. The blocks were dried and weighed as described on experiment 1. This experiment included 30 replications.

Wood consumption was measured by replacing the wood blocks every 2 mo and weighing the consumed blocks after drying them by using the procedure described above. Observations were made every 10 d for mortality. Only the death of the whole group within a dish was recorded, individual termite mortality was not measured to minimize disruption. This experiment proceeded for 6 mo under the environmental conditions described for experiments 1 and 2. The length of the experiment was determined by the survival of the termite groups feeding on the resistant wood species. The mean consumption rate in milligrams per day was compared between treatments by using the contrast option of the GLM procedure of JMP software (SAS Institute 1995). The mean consumption in grams during the first 60-d period was also compared between treatments using this procedure. The survival of small groups was compared by using the *Z*-test.

Results

Feeding Preferences of Selected Commercial Wood Species. Birch was consumed at the highest rate and this difference was highly significant ($F = 53.76$; df = 23, 456; $P < 0.0001$) (Table 2). Consumption rates showed that the five most preferred wood species were yellow birch; red gum, *Liquidambar styraciflua* L.; Parana pine, *Araucaria angustifolia* (Bert.); sugar maple, *Acer saccharum* Marsh.; and pecan, *Carya illinoensis* (Wangenh.), in order of preference. Differences among consumption rates of these five species were significant ($|T| > 1.68$, df = 456, $P < 0.095$) (Table 2). A group of wood species that included northern red oak, *Quercus rubra* L.; yellow poplar, *Liriodendron tulipifera* L.; American ash, *Frexinus americana* L.; Douglas fir, *Pseudotsuga menziesii* (Mirb.); and southern yellow pine was significantly less preferred by the Formosan termite. Difference in consumption among these species was not significant except between red oak and yellow pine (Table 2). The rest of the wood species showed little consumption by the Formosan termite and no significant differences were observed among them. The total consumption of each wood species by 20 *C. formosanus* groups in four repetitions lasting 40 d each is presented in Fig. 2A. No differences in feeding preferences were observed between replications.

Response to Less Preferred Wood Species. Experiment 2 showed a better resolution of the feeding preference gradients among the less preferred wood species in experiment 1. Ponderosa pine (*Pinus ponderosa* Laws.) and western red cedar heartwood

Table 2. Mean consumption rates (mg/d) of 24 wood species by *C. formosanus* in multiple-choice feeding studies of selected commercial wood species

Wood species[a]	Consumption rate[b,c]	% consumed[b]
Bir	47.88 ± 4.30a	40.77 ± 3.49
ReG	32.43 ± 2.92b	33.83 ± 1.24
PaP	25.77 ± 3.77c	26.38 ± 3.96
Map	21.78 ± 3.03d	20.77 ± 3.03
Pec	15.09 ± 1.94e	11.23 ± 1.52
ReO	10.17 ± 1.40f	8.97 ± 1.24
YeP	7.13 ± 1.28fg	8.15 ± 1.56
Ash	6.28 ± 1.24fgh	6.77 ± 1.36
DoF	6.09 ± 1.00fgh	6.79 ± 1.11
SYP	5.13 ± 1.16ghi	6.07 ± 1.40
WhO	3.11 ± 0.62hij	2.98 ± 0.62
Bal	2.54 ± 0.42hij	13.69 ± 2.21
Wal	1.70 ± 0.35ij	1.74 ± 0.34
BaC	1.43 ± 0.21ij	1.99 ± 0.31
Che	1.29 ± 0.36ij	1.54 ± 0.46
Bas	1.00 ± 0.17j	1.33 ± 0.24
PoP	0.99 ± 0.35j	1.19 ± 0.40
ReW	0.49 ± 0.13j	0.71 ± 0.17
Sas	0.33 ± 0.07j	0.38 ± 0.08
SiC	0.27 ± 0.10j	0.31 ± 0.10
SpC	0.21 ± 0.06j	0.27 ± 0.07
WRC	0.18 ± 0.09j	0.31 ± 0.15
Mah	0.06 ± 0.04j	0.06 ± 0.04
InR	0.02 ± 0.01j	0.02 ± 0.01

[a] Species three-letter codes are defined in Table 1.
[b] Mean ± SE, $n = 80$.
[c] Means with the same letter are not significantly different after GLM contrast t-test ($\alpha = 0.05$; $F = 53.76$; df = 23, 456; $P < 0.0001$).

showed the highest consumption followed by bald cypress (Table 3). Differences between the first two species and bald cypress were significant ($|T| = 2.51$ and 2.25, df = 416, $P = 0.0125$ and 0.0251, respectively). A five-species group consisting of honey locus, basswood (*Tilia americana* L.), 9-y environmentally exposed Alaskan yellow cedar, redwood [*Sequoia sempervirens* (D. Don)], and black cherry (*Prunus serotina* Ehrh.) showed significantly lower consumption than bald cypress but no significant differences among themselves (Table 3). The rest of the species were significantly less consumed ($|T| > 2.2$, df = 416, $P < 0.023$) by the Formosan termite, but no statistical differences were observed among these 14 species (Table 3). Fig. 2B shows the consumption of each wood species by 20 artificial nests of *C. formosanus* in four repetitions lasting 40 d each.

Natural Resistance of Least Preferred Wood Species. All the wood species tested in experiment 3 induced higher mortality than the two control species (southern yellow pine and yellow birch) (Table 4). After 1 mo, all treatments except sinker cypress and Alaskan yellow cedar showed significantly higher mortality than the two controls. After 2 mo, all treatments showed significantly higher mortality than yellow birch and southern yellow pine (after Z-test at $\alpha = 0.05$, with $Z > 1.96$ and df = 58) (Table 4). Most treatments, except sinker cypress and western red cedar, showed no survivors after 3 mo and all except sinker cypress had no survivors by the fourth month. The two control treatments, southern yellow pine and yellow birch, showed 93.3 and 90% survival respectively after 4 mo (Table 4).

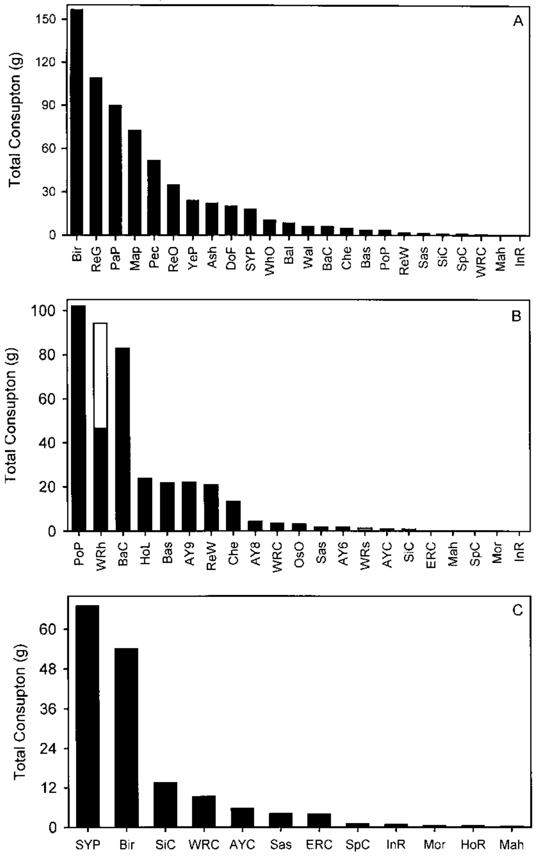

Fig. 2. Total wood consumption by groups of *C. formosanus* in three experiments. (A) Experiment 1 is a multiple-choice feeding test of commercial woods consisting of 20 groups of 2,200 workers and 440 soldiers and four repetitions per group lasting 40 d each. (B) Experiment 2 is a multiple-choice feeding test of less preferred wood species with the same number of groups and repetitions as experiment 1; except for heartwood (WRh) and sapwood (WRs) treatments, which had only 10 groups each. Blank bars in B indicate the amount of wood expected to be consumed if these treatments had balanced numbers. (C) Experiment 3 is a no-choice test consisting of 30 groups of 200 workers and 50 soldiers per each of 12 wood species lasting 120 d each. See Table 1 for abbreviations of species.

During the first 2 mo, termites of all treatments consumed wood at significantly lower rates than the two control groups ($F = 91.26$; df = 11, 348; $P < 0.0001$). Termites consumed southern yellow pine wood at significantly higher rates (19.3 ± 6.1 mg/d) than birch (16.0 ± 5.9 mg/d) ($T = 3.57$, df = 348, $P = 0.0004$) (Table 5). The treatments that showed the highest consumption (after the controls) were sinker cypress and western red cedar with 7.1 ± 5.9 and 5.4 ± 6.4 mg/d, respectively. The difference in consumption between these two treatments was significant ($T = 1.77$, df = 348, $P = 0.078$). Consumption of western red cedar was significantly higher than Alaskan yellow

Table 3. Mean consumption rates (mg/d) of 22 wood choices by *C. formosanus* in multiple-choice feeding test of less preferred wood species

Wood species[a]	Consumption rate[b,c]	% consumed[b]
PoP	32.38 ± 3.63a	37.59 ± 4.35
WRh	30.17 ± 3.94a	49.24 ± 6.52
BaC	26.87 ± 2.41b	36.03 ± 3.33
HoL	7.53 ± 1.31c	7.75 ± 1.39
Bas	6.99 ± 1.06c	8.59 ± 1.44
AY9	6.94 ± 1.35c	9.41 ± 1.82
ReW	6.51 ± 1.26c	11.33 ± 2.17
Che	4.37 ± 0.52cd	4.69 ± 0.57
AY8	1.48 ± 0.28de	1.89 ± 0.38
WRC	1.26 ± 0.46de	2.28 ± 0.82
OsO	1.02 ± 0.23de	0.96 ± 0.20
Sas	0.59 ± 0.23e	0.57 ± 0.23
AY6	0.56 ± 0.22e	0.67 ± 0.27
WRs	0.40 ± 0.08e	0.82 ± 0.16
AYC	0.26 ± 0.06e	0.43 ± 0.11
SiC	0.24 ± 0.12e	0.28 ± 0.14
ERC	0.07 ± 0.05e	0.08 ± 0.05
Mah	0.02 ± 0.01e	0.02 ± 0.02
SpC	0.01 ± 0.01e	0.02 ± 0.01
Mor	0.01 ± 0.01e	0.01 ± 0.01
InR	0.01 ± 0.01e	0.01 ± 0.004
HoR	0.00e	0.00

[a] Species three-letter codes are defined in Table 1.
[b] Mean ± SE, n = 80 except WRh and WRs with n = 40.
[c] Means with the same letter are not significantly different after GLM contrast t-test ($\alpha = 0.05$; $F = 43.59$; $df = 21, 416$; $P < 0.0001$).

cedar ($T = 1.93$, df = 348, $P = 0.054$) (Table 5). The lowest consumption was observed in treatments Spanish cedar, Honduras mahogany, Honduras rosewood, morado, and Indian rosewood during the first 2-mo period and no consumption was observed in these treatments during the second 2-mo period.

Wood consumption decreased significantly during the second 2-mo period in the eastern red cedar ($T = 2.49$, df = 32, $P = 0.018$), AYC ($T = 6.53$, df = 34, $P < 0.0001$), and sassafras ($T = 3.11$, df = 32, $P = 0.004$) treatments compared with the first 2-mo period in these treatments. No significant change in consumption was observed in the treatments western red cedar, sinker cypress, southern yellow pine, and yellow birch between the first and second 2-mo periods (Table 5). Statistical comparison of consumption between 2-mo periods was not possible for treatments Spanish cedar, Honduras mahogany, Indian rosewood, Honduras rosewood, and morado because only one nest survived in each of these treatments to the second 2-mo period. Total consumption of each wood species by 360 groups of 250 *C. formosanus* during a period of 120 d is presented in Fig. 2C.

Table 4. Percentage of mortality of 250-individual groups of *C. formosanus* fed with 12 wood species in no-choice tests

Wood species[a]	Age in days			
	30	60	90	120
Mah	46.7a	96.7a	100.0a	100.0a
SpC	36.7ab	96.7a	100.0a	100.0a
InR	40.0ab	96.7a	100.0a	100.0a
HoR	30.0abc	96.7a	100.0a	100.0a
Mor	30.0abc	96.7a	100.0a	100.0a
ERC	30.0abc	86.7ab	100.0a	100.0a
Sas	20.0bcd	86.7ab	100.0a	100.0a
AYC	3.3e	80.0bc	100.0a	100.0a
WRC	20.0bcd	66.7bc	96.7b	100.0a
SiC	13.3cde	63.3c	86.7b	96.7b
Bir	6.7de	10.0d	10.0c	10.0c
SYP	3.3e	3.3d	3.3c	6.7c

Percentages with the same letter are not significantly different after Z-test at $\alpha = 0.05$, $n = 30$.
[a] Species three-letter codes are defined in Table 1.

Table 5. Consumption rates (mg/d) of 250-individual groups of *C. formosanus* fed with 12 wood species in no-choice tests

Wood species[a]	n	2-mo periods		
		0–60[b]	n	61–120[b]
SYP	30	19.3 ± 6.1a	29	18.7 ± 4.3
Bir	30	16.0 ± 5.9b	27	15.8 ± 3.2
SiC	30	7.1 ± 5.9c	11	3.7 ± 5.1
WRC	30	5.4 ± 6.4d	10	2.0 ± 2.2
AYC	30	3.6 ± 1.3e*	6	0.08 ± 0.1
ERC	30	2.9 ± 1.7e*	4	0.7 ± 0.8
Sas	30	2.8 ± 1.4e*	4	0.6 ± 0.7
SpC	30	1.1 ± 0.7f	1	0.0
Mah	30	0.4 ± 0.3f	1	0.0
HoR	30	0.5 ± 0.4f	1	0.0
Mor	30	0.5 ± 0.5f	1	0.0
InR	30	0.8 ± 1.5f	1	0.0

Mean ± SE. Means with * within rows are significantly higher after t-test ($\alpha = 0.05$).
[a] Species three-letter codes are defined in Table 1.
[b] Means with the same letter within columns are not significantly different after GLM contrast ($\alpha = 0.05$).

Discussion

This study shows that six wood species (five hardwoods) were significantly more preferred by Formosan subterranean termites than southern yellow pine. Use of any of these wood species within monitoring tools would probably improve detection of these termites. Traditional use of southern yellow pine, either in stakes or monitoring bucket traps, may reduce the chances of detecting Formosan subterranean termite activity if other more preferred wood sources are available in the area. Observations of foraging behavior in this study's multiple-choice arenas revealed that workers tend to reject less preferred wood blocks and seal the access with mud and carton. Termites were observed sealing the access to southern yellow pine and yellow poplar wood blocks in at least 30% of the repetitions of experiment 1. Southern yellow pine stakes may be rejected similarly in the field if a large source of highly preferred wood (i.e., trees of preferred species) is present within the foraging range of the termites.

However, it is important to consider that there are three pine species that are commercialized under the name of southern yellow pine (Grimm 1983). Only one of them was tested in this study, but future studies will focus on differences in Formosan termite preferences among pine species. In addition, southern yellow pine did not show feeding deterrence in experiment 3. When presented with no-choice, Formosan subterranean termites consume more yellow pine than birch (Table 5; Fig. 2). Comparison of total consumption of some wood species by the Formosan subterranean termites between choice and no-choice studies provides an idea of the complexity of the feeding preferences of this termite (Fig. 2). The rate of consumption of any particular wood in the field by the Formosan subterranean termite will be greatly dependent on the existing choices.

The wood species that showed the lowest preference by the Formosan subterranean termite in experiment 2 also were shown to cause death to these termites in experiment 3. Experiment 2 is a multiple-choice experiment designed to determine feeding preference, whereas experiment 3 is a no-choice test designed to establish feeding deterrence. Termite mortality in a no-choice test may be induced by toxicity or starvation induced by a strong feeding deterrence (Scheffrahn 1991). This may be an indication that negative food preference in Formosan subterranean termites may be mediated by the presence of noxious compounds in the food source. Scheffrahn (1991) stated that resistance of wood to termite attack is mainly determined by the presence of chemicals in the linocellulosic tissue.

Sinker cypress was significantly less preferred than bald cypress; however, both of those woods belong to the same species, *Taxodium distichum.* Bald cypress is commercially available but consists mostly of sapwood. Sinker cypress is a commercial name given to old (aged) trees (mostly heartwood) that have been recovered after years of remaining under water in Louisiana swamps. The commercial availability of sinker cypress is limited. Gas chromatograph studies showed that sinker cypress has 26 times higher concentration and three times higher diversity of terpenoids than bald cypress (M.G.R., unpublished data). Scheffrahn et al. (1988) identified ferruginol and manool in bald cypress heartwood as the compounds responsible for termite feeding deterrence.

Western red cedar sapwood showed significant natural resistance to the Formosan termite. Heartwood of western red cedar was susceptible and significantly more preferred than bald cypress, basswood, and redwood. The presence of insect feeding deterrents has been reported in the foliage of western red cedar (Alfaro et al. 1981) and wood extractives of western red cedar have been shown to be significantly toxic to the eastern subterranean termite (Carter 1976).

Alaskan yellow cedar showed significant natural resistance to Formosan termites and was significantly less preferred than bald cypress and redwood. Grace and Yamamoto (1994) observed mortality and feeding deterrence on small colonies of *C. formosanus* when presented with Alaskan yellow cedar. In this study, Alaskan yellow cedar induced significantly higher feeding deterrence to Formosan termites than western red cedar and sinker cypress (Table 5). This result is highly encouraging because this wood species is of great commercial value and suitable for construction (McDonald et al. 1997). In the multiple-choice feeding test, there was no significant difference in preference for 6- to 8-yr-old, and new Alaskan yellow cedar, indicating that the properties of this wood do not deteriorate after 8 yr of storage. Exposure to the elements for 9 yr in British Columbia significantly affected the properties of Alaskan yellow cedar. However, 9-yr exposed Alaskan yellow cedar was significantly less preferred than bald cypress, western red cedar heartwood, and ponderosa pine, and there was no significant difference in preference among 9-yr exposed Alaskan yellow cedar, black cherry, redwood, basswood, and honey locust. Exposure to the environment can diminish wood natural resistance by changing its chemical and physical characteristics through exposure to rain, sunlight, and microorganisms (Bultman and Southwell 1976). Deterioration of Alaskan yellow cedar may proceed faster in warmer climates, but the use of this wood species has not been widespread and data are not available at present. More studies should be conducted on the effect of warmer environments on the deterioration of Alaskan yellow cedar termite-resistance properties.

Sassafras was the only North American hardwood to show significant natural resistance to the Formosan termite. In this study, feeding deterrence induced by sassafras was statistically similar to that induced by Alaskan yellow cedar. Carter and Dell (1981) reported that sassafras and osage orange exhibit natural resistance to native subterranean termites. Carter and Dell (1981) also reported moderate resistance in honey locust, black cherry, and black walnut to *R. flavipes.* In our tests, Formosan termites showed significantly lower preference for of all those species as compared with bald cypress and sinker cypress.

Five tropical wood species, including Spanish cedar, Honduras mahogany, Indian rosewood, Honduras rosewood, and morado, showed significantly higher feeding deterrence than Alaskan yellow cedar, eastern red cedar, and sassafras. Hexane extracts of Spanish cedar have been reported to be toxic to Formosan subterranean termites (Carter and de Camargo 1983). Mahogany has been reported to be termite resistant by Bultman and Southwell (1976). There are only brief reports on the termite resistance of Indian rosewood in India and Honduras rosewood in Honduras (Jacobson 1975) and no previous report could be found on the resistance of morado to subterranean termites. These five tropical wood species are expensive and rare and therefore not suitable for use in construction in the United States. Their value to termite research is in their chemistry as potential new sources of toxicants or growth regulators.

Acknowledgments

We acknowledge the valuable technical assistance of Patrick Plaisance. We thank Peter Fisher and Peter Fitzpatrick for providing Alaska yellow cedar samples, and Joseph A. Lipovsky for providing samples of honey locust and Osage orange. We also thank the personnel of Riverside Lumber, New Orleans, LA, for providing information about the commercial wood species.

References Cited

Alfaro, R. I., H. D. Pierce, Jr., J. H. Borden, and A. C. Oehlschlager. 1981. Insect feeding and oviposition deterrents from Western red cedar foliage. J. Chem. Ecol. 7: 39–48.

Beal, R. H. 1987. Introduction of *Coptotermes formosanus* Shiraki to the continental United States, pages 48–53. *In* M. Tamashiro and N. Y. Su [eds.], Biology and control of the Formosan subterranean termite. Research and Extension series 083. College of Tropical Agriculture and Human Resources, University of Hawaii, Honolulu, HI.

Bultman, J. D., and C. R. Southwell. 1976. Natural resistance of tropical American woods to terrestrial wood-destroying organisms. Biotropica 8: 71–95.

Carter, F. L. 1976. Responses of subterranean termites to wood extractives. Mater. Organis 11 (suppl.): 357–364.

Carter, F. L., and C.R.R. de Camargo. 1983. Testing antitermitic properties of Brazilian woods and their extracts. Wood Fiber Sci. 15: 350–357.

Carter, F. L., and T. R. Dell. 1981. Screening selected American hardwoods for natural resistance to a native subterranean termite, *Reticulitermes flavipes* (Kollar). USDA For. Serv. Res. Pap. SO-176.

Edwards, R., and A. E. Mill. 1986. Termites in buildings. Rentokil Limited, Felcourt, East Grinstead, UK.

Grace, J. K., and R. T. Yamamoto. 1994. Natural resistance of Alaskan-cedar redwood, and teak to Formosan subterranean termites. For. Prod. J. 44: 41–45.

Grimm, W. C. 1983. The illustrated book of trees. Stackpole Books, Mechanicsburg, PA.

Jacobson, M. 1975. Insecticides from plants: a review of literature, 1954–1971. U.S. Dep. Agric. Agric. Res. Serv. Agric. Handb. 461.

La Fage, J. P. 1987. Practical considerations of the Formosan subterranean termite in Louisiana: a 30-year-old problem, pages 37–42. *In* M. Tamashiro and N. Y. Su [eds.]. Biology and control of the Formosan subterranean termite. Research and Extension series 083. College of Tropical Agriculture and Human Resources, University of Hawaii, Honolulu, HI.

Mannesmann, R. 1973. Comparison of twenty-one commercial wood species from North America in relation to feeding rates of the Formosan termite, *Coptotermes formosanus* Shiraki. Mater. Org. 8: 107–120.

McDonald, K. A., P. E. Hennon, J. H. Stevens, and D. W. Green. 1997. Mechanical properties of salvaged dead yellow-cedar in southeast Alaska. USDA For. Serv. Res. Pap. FPL-RP-565.

McMichael, J. A. 1998. Survey of subterranean termites (Isoptera: Rhinotermitidae) in trees in Sam Houston Jones State Park, West Lake, Louisiana. M.S. thesis, Louisiana State University, Shreveport.

SAS Institute. 1995. JMP statistics and graphics guide, version 3. SAS Institute, Cary, NC.

Scheffrahn, R. H. 1991. Allelochemical resistance of wood to termites. Sociobiology 19: 257–281.

Scheffrahn, R. H., R.-C. Hsu, N.-Y. Su, J. B. Huffman, S. L. Midland, and J. J. Sims. 1988. Allelochemical resistance of bald cypress, *Taxodium distichum,* Heartwood to the subterranean termite, *Coptotermes formosanus.* J. Chem. Ecol. 14: 765–776.

Smythe, R. V., and F. L. Carter. 1969. Feeding responses to sound wood by the eastern subterranean termite, *Reticulitermes flavipes.* Ann. Entomol. Soc. Am. 62: 335–337.

Smythe, R. V., and F. L. Carter. 1970a. Feeding responses to sound wood by *Coptotermes formosanus, Reticulitermes flavipes,* and *R. virginicus* (Isoptera: Rhinotermitidae). Ann. Entomol. Soc. Am. 63: 841–847.

Smythe, R. V., and F. L. Carter. 1970b. Survival and behavior of three subterranean termite species in sawdust of eleven wood species. Ann. Entomol. Soc. Am. 63: 847–850.

Su, N. Y., and R. H. Scheffrahn. 1988. Foraging population and territory of the Formosan subterranean termite (Isoptera: Rhinotermitidae) in urban environment. Sociobiology 14: 353–359.

Su, N. Y., and R. H. Scheffrahn. 1990. Economically important termites in the United States and their control. Sociobiology 17: 77–94.

Su, N. Y., and M. Tamashiro. 1986. Wood-consumption rate and survival of the Formosan subterranean termite (Isoptera: Rhinotermitidae) when fed on six woods used commercially in Hawaii. Proc. Hawaii. Entomol. Soc. 26: 109–113.

Su, N. Y., and M. Tamashiro. 1987. An overview of the Formosan subterranean termite (Isoptera: Rhinotermitidae) in the world, pages 3–15. *In* M. Tamashiro and N. Y. Su [eds.], Biology and control of the Formosan subterranean termite. Research and Extension series 083. College of Tropical Agriculture and Human Resources, University of Hawaii, Honolulu, HI.

Waller, D. A., C. G. Jones, and J. P. La Fage. 1990. Measuring wood preference in termites. Entomol. Exp. Appl. 56: 117–123.

Received for publication 14 September 2000; accepted 26 December 2000.